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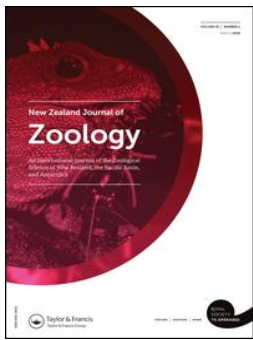
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RESEARCH ARTICLE



Effects of the presence of zoo visitors on zoo-housed little penguins (*Eudyptula minor*)

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ABSTRACT

Little penguins (*Eudyptula minor*), or Kororā in Māori, show variation in their behavioural responses towards zoo visitors in Australian zoos. We experimentally examined the effects of visitor presence on the behaviour and stress physiology of little penguins at Wellington Zoo, New Zealand. The two treatments were: (1) Visitor presence – the exhibit was open to visitors; and (2) Visitor absence – the exhibit was closed to visitors. We found that when the exhibit was closed to visitors, the percentage of penguins observed close to the visitor viewing pier increased from about 1% to 9%, but there was little effect on other behaviours and faecal glucocorticoid metabolite concentrations. This result of increased avoidance of the visitor viewing pier when the exhibit was open to visitors suggests close visitor contact, particularly from above, may be fear-provoking for these penguins. We conclude that designing enclosures to allow close viewing proximity of visitors, such as visitors looming over the pool, may be futile in improving visitor experience, since this species of penguins is likely to avoid these types of viewing areas when visitors are present. Visitors positioned close to and above penguins may be particularly problematic since visitors in this position may be perceived as threatening.

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Introduction

Little penguins (*Eudyptula minor*), also known as blue, little blues or Kororā in Māori, are the smallest species of penguins and endemic to the southern parts of Australia and New Zealand (Stahel and Gales 1987; BirdLife International 2020). Globally, the conservation status of little penguins is ‘Least Concern’ but, there is evidence of declining wild population numbers (Williams et al. 2009; Smith 2013; Robertson et al. 2017; BirdLife

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International 2020). In Australia, numerous little penguin colonies have shown substantial decline over the past several decades (Dann 1992; Stevenson and Woehler 2007; Colombelli-Négrel 2015; BirdLife International 2020). In New Zealand, populations are also showing signs of decline and so, are considered ‘at risk’ (Heber et al. 2008; Robertson et al. 2017; BirdLife International 2020). This general decline in wild little penguin populations across Australia and New Zealand is driven by various factors such as predation by introduced species (e.g. foxes (*Vulpes vulpes*), domesticated dogs (*Canis lupus familiaris*), feral cats (*Felis catus*)), climate variability, habitat loss and human disturbance (Dann and Norman 2006; Agnew et al. 2013; BirdLife International 2020). In particular, there is growing concern of the negative effects associated with increased human presence from wildlife tourism and other human disturbances on little penguin behaviour, reproductive success and population size (Carney and Sydeman 1999; Shaughnessy and Briggs 2009; Higham and Shelton 2011; Tisdell and Wilson 2012; Colombelli-Négrel 2015; Rodríguez et al. 2018). For example, weekly nest box inspections by researchers and the close proximity of visitors were found to reduce burrow occupancy and hatching success in little penguin colonies on Penguin Island, Western Australia (Klomp et al. 1991; Wienecke et al. 1995). Similarly, areas of high human traffic and visitor paths, particularly those also utilised by arriving penguins, were found to increase nest displacement and reduce the number of little penguins landing in those areas of the beach (Weerheim et al. 2003; Giling et al. 2008; Shaughnessy and Briggs 2009). In contrast, some studies have suggested minimal effect of human disturbances on the breeding success and survival rates of little penguins when disturbances are relatively low or well-regulated (Dann 1992, 1994; Rogers et al. 1995; Perriman and Steen 2000; Shaughnessy and Briggs 2009; Wiebkin 2011; Agnew and Houston 2020). This variation in the reported literature on the effects of human disturbances on little penguins shows the need for further research to understand how penguins perceive human presence. By understanding this relationship between humans and penguins, it will aid the development of appropriate strategies to manage human-penguin interactions and safeguard the welfare of penguins.

Most research to date on the effects of human disturbances on wild little penguins has been on colonies in Australia, despite little penguins also being a highly valued and a protected native species in New Zealand. Only one study, to our knowledge, has been conducted on wild little penguins in New Zealand. No detrimental effect of human disturbances was found on the reproductive success of the Oamaru Blue Penguin Colony which was exposed to tourists compared to the Oamaru Creek Penguin Refuge that had no public access (Agnew and Houston 2020). This was likely the result of the tourism operation at the Oamaru Blue Penguin Colony implementing strategies to regulate human disturbances such as reduced noise, light and movement from visitors and restricted visitor viewing areas; effects that are consistent with past research (Dann 1992; Rogers et al. 1995; Shaughnessy and Briggs 2009; Wiebkin 2011; Agnew and Houston 2020). Also, this research adds to the growing evidence that little penguins, found at different locations, may respond to visitors in a similar manner if the nature of visitor contact is the same (Klomp et al. 1991; Weerheim et al. 2003; Giling et al. 2008; Carroll et al. 2016). However, penguin responses may vary as a result of characteristics of the environment differing at each location which may influence the nature of visitor contact. This is beginning to be observed

in research on the effect of visitors on zoo-housed little penguins which has also focused, thus far, only on Australian zoo-housed little penguins (Sherwen et al. 2015; Chiew, Butler, et al. 2019; Chiew et al. 2020).

Behaviours such as huddling, vigilance and in particular avoidance, have been widely documented as indicators of fear of humans in animals and linked with physiological correlates of fear such as increased blood glucocorticoid and glucocorticoid metabolite (GM) concentrations (Gray 1987; Hemsworth and Coleman 2011; Hemsworth et al. 2018; Sherwen and Hemsworth 2019). The physiological stress response to challenges nearly always includes activation of the sympatho-adrenal medullary system and the hypothalamo–pituitary–adrenal axis, with the consequent increase in synthesis of catecholamines and glucocorticoids, respectively (Sapolsky 2002; Tilbrook and Ralph 2018). Any free (unbound) glucocorticoids are excreted through the urine or faeces which can then be sampled to measure GM concentrations (Möstl and Palme 2002; Palme et al. 2005; Sheriff et al. 2010). Faecal glucocorticoid metabolite (FGM) concentrations are a commonly used measure of physiological stress in zoo animals, including zoo-housed penguins, because of its non-invasive sampling technique and ability to reliably reflect plasma glucocorticoid concentrations (Shepherdson et al. 2004; Sheriff et al. 2010, 2011; Ozella et al. 2015; Chiew, Butler, et al. 2019; Palme 2019; Scheun et al. 2020). Consequently, using both behavioural and physiological measures of fear of humans in animals allows for a more robust assessment of the effect humans on zoo-housed penguin welfare.

While still limited, there is evidence from studies in Australian zoos that close visitor contact may be fear-provoking for zoo-housed little penguins. Sherwen et al. (2015) found increases in huddling, vigilance, aggression and avoidance and reductions in swimming by little penguins when visitors were present at Melbourne Zoo (Victoria, Australia). Similarly at the same zoo, Chiew, Butler, et al. (2019) found that close visitor viewing proximity primarily influenced little penguin fear responses. However, increased separation between visitors and the penguins using a physical barrier reduced these fear responses (Chiew, Butler, et al. 2019). Also, little penguins at Taronga Zoo (New South Wales, Australia) showed some avoidance of visitors, indicated by the aversion of the area near the main visitor viewing window when visual contact with visitors was not obstructed, and the preference for an area not visible to visitors (Chiew et al. 2020). The response by the little penguins at Taronga Zoo was suggested to be less pronounced than that at Melbourne Zoo because of the different enclosure designs that altered the nature of visitor contact, particularly in regard to the intensity of visitors (Chiew et al. 2020). These three studies on the effects of visitors on zoo-housed little penguins at two Australian zoos demonstrate the possible risk factors such as environment characteristics (e.g. enclosure design and management) that influence visitor-penguin interactions. However, further research is still required to fully comprehend the similarities or variation in little penguin fear responses towards visitors and the factors that influence the interactions between visitors and penguins across zoos.

Research has suggested that there are two congeneric taxa of little penguins; *Eudyptula novaehollandiae* being little penguins occurring in Australia and south east New Zealand (Otago) and *Eudyptula minor* being little penguins occurring in all other parts of New Zealand (Peucker et al. 2009; Grosser et al. 2015, 2016, 2017). This genetic difference

has been suggested to be linked to some morphological and behavioural differences between these two distributions of little penguins (Grosser et al. 2015, 2017). For example, it has been reported that Australian little penguins commonly come ashore after dusk in 'rafts' where they swim ashore in groups, walk together to their nest areas and are capable of double brooding (Grosser et al. 2015). These behaviours have not been as frequently observed in the New Zealand lineage of little penguins potentially because of genetic differences. However, these behavioural differences could also be due to lower population numbers of New Zealand lineage colonies in comparison to the Australian colonies, or due to the generally limited monitoring efforts over large parts of New Zealand (Dann 1994; BirdLife International 2020; Cargill et al. 2020). In Wellington (New Zealand), little penguins have been identified to be genetically different from Australian little penguins (i.e. *Eudyptula minor* lineage), with some degree of hybrid ancestry in this population (Grosser et al. 2015). Therefore, the little penguins in the present experiment may have differed genetically from the little penguins studied in Australian zoos. Anecdotally, zoo staff at Wellington Zoo also suggested that the little penguins in their zoo were more pair driven, less colony driven and shyer than Australian little penguins (M. Forbes and S. Eyre, pers. comm., 2018). Hence, further examination to determine the extent in which the effects of visitors on *Eudyptula novaehollandiae* are reflected in *Eudyptula minor*, both in the wild and in captive settings like zoos is needed.

The present experiment investigated the effects of visitor presence at the little penguin exhibit at Wellington Zoo (Wellington, New Zealand) on penguin behaviours indicative of fear such as avoidance, huddling and vigilance, and on the stress physiology of the penguins. This research will help improve the management of visitor-penguin interactions both in zoos and in the wild.

Methodology

Study species, housing and husbandry

This research was approved by the Victoria University of Wellington Animal Ethics Committee (approval number 25504) and was conducted at Wellington Zoo's Meet the Locals – He Tuku Aroha little penguin enclosure (Wellington, New Zealand). This 225 m² enclosure consists of a large pool that is surrounded by a pebble shoreline, trees, rocks, and shrubs as well as a partially upturned boat for shelter and five nest boxes (Figures 1–3). The visitor viewing area consists of a viewing pier that extends 2 m out over a proportion of the pool and an area along one side of the exhibit which is surrounded by a 1 m tall wooden fence and a visitor pathway approximately 4.2 m wide (Figures 1–3). Visitors also have opportunities to view the penguins from a visitor viewing hide at the back of the enclosure where the penguins' view of visitors is obstructed (Figures 1–3). However, preliminary observations found that this hide was rarely used by visitors. During the study, the enclosure housed six wild-born little penguins (three males and three females) rescued from the wild in New Zealand due to sustained injuries (e.g. blind in one eye, loss of one wing or eye). Four of the birds came from the Wellington coast, one from Nelson and one from Whanganui. They were fed at 9:00 h and 15:00 h each day. The afternoon feeding was accompanied by a keeper

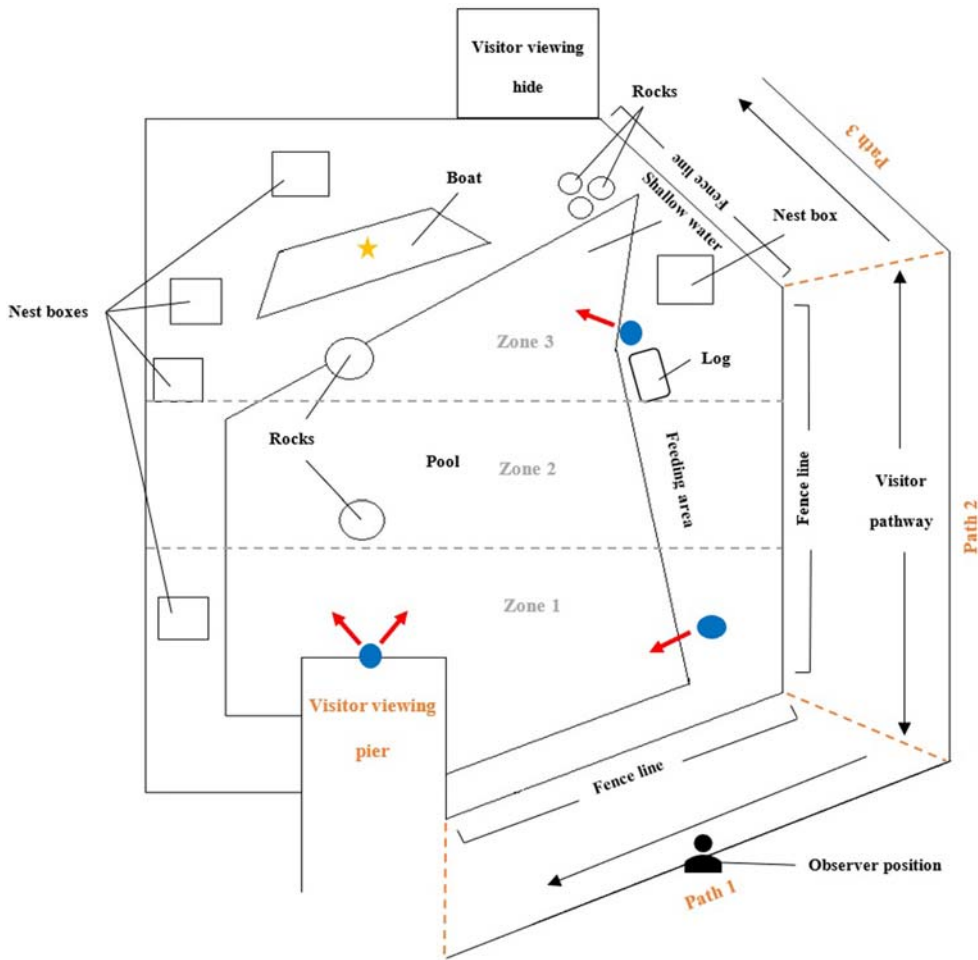


Figure 1. Schematic of the little penguin exhibit at Wellington Zoo. The blue circles represent the position of the cameras, the red arrows indicate the direction of the cameras and the star represents the position where an extra camera was placed. The orange dotted lines show the division of the visitor viewing area into four sections in the exhibit: the Visitor viewing pier and Paths 1, 2 and 3 (in orange). The grey dotted lines delineate the Zones 1, 2 and 3 in the enclosure in which the position of the penguins was observed relative to the visitor viewing pier.

presentation where visitors watched from outside the enclosure, primarily from the visitor viewing pier and Path 1 (Figure 1). Husbandry followed normal routines and remained consistent throughout the course of the study.

Study design

A two treatment fully randomised design was used to examine the effects of visitor presence on little penguins. The two treatments were:

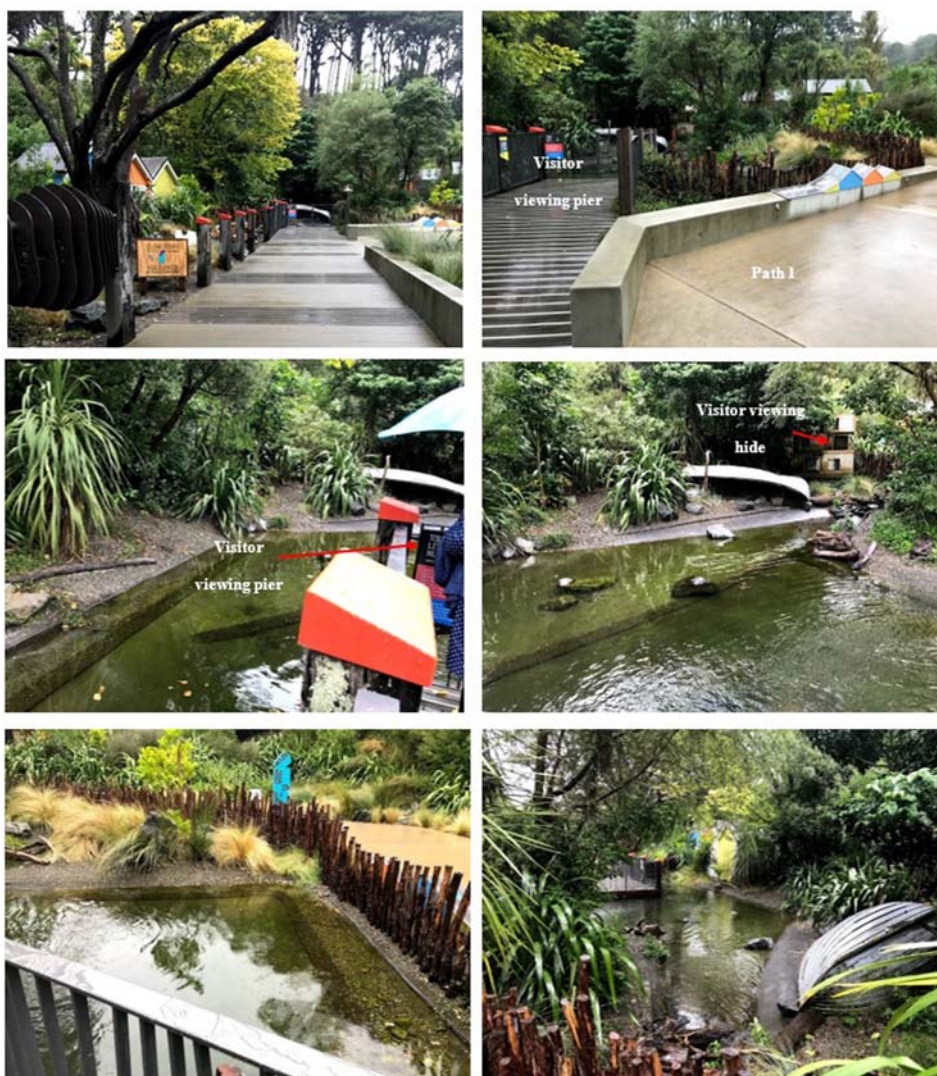


Figure 2. Meet the Locals – He Tuku Aroha, little penguin exhibit at Wellington Zoo.

- (1) *Visitor presence (Control)* – the exhibit was open to visitors as usual (standard zoo conditions).
- (2) *Visitor absence (Treatment)* – the penguin exhibit was closed to the public. Visitors were prevented from accessing the exhibit by closing two visitor access points. However, penguins could still hear but not see visitors at nearby exhibits of other animal species.

Each treatment was randomly imposed for 2-day periods, two imposition periods per week (Monday and Tuesday; Thursday and Friday), with five replicates of each treatment (total of 20 study days). The study was conducted over five weeks during May and June 2018 (Autumn–Winter). Weekends, public holidays and school holidays were avoided to circumvent the normal variation in visitor numbers that occurs on weekends and school/



Figure 3. **A**, The fence line and vegetation in Path 2 of the visitor viewing area. **B**, The fence line in Path 3 of the visitor viewing area and the visitor viewing hide.

public holiday periods. One week out of the five weeks had treatments with no day separation between the two imposition periods because a public holiday occurred on the Monday.

Animal behavioural observations

Four HERO 5 GoPro cameras were placed around the enclosure, covering the main areas utilised by the penguins to record penguin numbers and behaviours indicative of fear between 08:45 and 16:00 h (Table 1). Only three of the four cameras were used for behavioural observations and analysis as the fourth camera was only used if the observer could not see penguins under the boat clearly from the other cameras or had doubt in the behaviour(s) displayed under the boat. Despite the penguins being distinguishable by their physical features, observation of the camera footage was not able to clearly discern these physical differences and so, penguin behaviour was recorded at the group level.

Penguin behavioural data were transcribed during the playback of video footage on all study days in 3×1 h observation blocks (10:30–11:30 h, 12:00–13:00 h, 13:30–14:30 h). Instantaneous point sampling and one-zero sampling were used for behavioural patterns that were considered states (i.e. of an appreciable duration) and events (i.e. relative short durations), respectively (Table 1). Instantaneous point sampling at 3 min intervals recorded the number of visible penguins in each behavioural state and one-zero sampling in 30 s periods, within each 3 min interval, was used to record the number of visible penguins displaying each behavioural event. The visitor viewing pier was identified during preliminary observations to be the main viewing area for visitors, based on visitor numbers. Paths 1, 2 and 3 were generally where visitors walked and the penguins' view of visitors in these sections were markedly obstructed by the vegetation between the pathway and penguins in the exhibit, especially in Paths 2 and 3 (Figures 1–3). Therefore, the enclosure was divided into three zones based on the distance from the visitor viewing pier: Zone 1 was 0–4 m, Zone 2 was 4–7 m and Zone 3 was greater than 7 m from the visitor viewing pier (Figure 1). The number of penguins visible in each zone

Table 1. Ethogram of penguin behaviour. Adapted from Chiew, Butler, et al. (2019) and Chiew et al. (2020).

Behaviour	Description
States	
Location in enclosure	Zone 1: 0–4 m from visitor viewing pier. Zone 2: 4–7 m from visitor viewing pier. Zone 3: greater than 7 m from visitor viewing pier.
Huddling (land)	Stationary, positioned within one wing distance of at least one other penguin.
Surface swimming	Moving or floating on the surface of the water, with head erect or in the water.
Diving	Moving under water surface.
Resting (land)	Belly on the ground, in a prone position, with eyes open or closed.
Idle (land)	Standing on two feet with a relaxed posture, eyes open or closed; not visually scanning environment.
Locomotion (land)	Upright position, moving from one location to another either by walking or running.
Vigilance (land)	Standing on two feet, visually scanning the environment with head movements from left to right or vice versa.
Events	
Preening (on land)	Running bill through plumage on land.
Preening (in water)	On the surface of the water and running bill through plumage.
Allopreening	Running bill through the plumage of another bird(s).
Agonistic interactions (maybe a combination of these behaviours)	Peck: Directed at another individual in which an individual directly hits or strikes at another bird with its bill. Lunge: sudden forward thrust of the body towards another individual. Chase: an individual runs after another individual. Threat: standing erect, approaching another individual, with wings spread back and head in a bowed/bent downward position (with or without vocalisations).
Bathing	In the water, twisting body from side to side in a shaking, rotary motion.
Body shake (land)	Standing on two feet, the body moves with a vigorous twisting motion causing the body to stretch up, the wings to move back and forth and the head to twist in a rotary movement with the body.
Head shake/flick (land)	Quick head movements from side-to-side on land.
Beak movement display (land)	Standing on two feet, with beak pointed directly upwards, opening and closing mouth.
Social interaction	Nibbling another individual's beak and/or slow touch of beaks.
Scratching (land/water)	Running foot through feathers, primarily head and neck area, in a quick up and down motion.
Other	Any other behaviour not described e.g. stretch, manipulate object

was also recorded. All behaviours were mutually exclusive except for 'location in enclosure' and 'huddling'.

Penguin faecal sampling and analysis: faecal glucocorticoid metabolites (FGM)

Faecal samples were collected by the principal investigator (SJC), adopting the methodology applied in Chiew, Butler, et al. (2019). Samples were collected at the end of each treatment day between 15:30 and 16:00 h and were immediately stored in a freezer at -20°C . Most samples were collected from the penguins' nest boxes which were known by keepers to be used by the same individual or pair of individuals each day. Therefore, samples collected from nest boxes were able to be identified to specific individuals or pairs. This ensured that samples were not biased by particular individuals or pairs. An average of 11 samples (range 3–18) were collected per day for the group of six penguins, for a total of 219 samples. Two samples were excluded due to being exceedingly small (i.e. weighing less than 0.005 g). Approximately 84% of the samples were collected from

known individuals or nest boxes, allowing us to ensure good sampling across the population.

Steroid extraction and assay procedures followed those previously described (Sherwen and Fanson 2015; Chiew, Butler, et al. 2019). FGM concentrations were measured and analysed using a double-antibody cortisone enzyme-immunoassay that has been biologically validated for little penguins (provided by R. Palme, University of Veterinary Medicine, Vienna, Australia) (Sherwen and Fanson 2015). Samples were assayed in duplicates and data are expressed as ng/g dried faeces for final concentrations. The intra-assay CV was less than 15% and inter-assay CV's were 5.62% and 10.04% for low and high controls, respectively.

Visitor behavioural observations

Visitor observations were conducted directly by the principal investigator (SJC) in seven 30 min observation blocks between 09:30 and 15:00 h. Instantaneous point sampling at 3 min intervals was used to record visitor number (number of adults and children within 1 m of enclosure) in each of the four sections of the visitor viewing area i.e. the Visitor viewing pier, Paths 1, 2 and 3 (Figure 1). Within each 3 min interval, visitor behavioural events were recorded continuously to record the total frequency of bouts of these behaviours (occurrences per observation block per day), irrespective of how many people were displaying the behaviours (Table 2). The visitor behavioural events were recorded to capture the types of behaviours visitors displayed while at the little penguin exhibit (Table 2). These observations were made from Path 1 of the visitor viewing area in a position that allowed full view of the visitor viewing area to record visitors in a manner that reduced the effect of the researcher's presence on the penguins (i.e. stationary or slow movement positioned 4.5 m from the enclosure; Figure 1). It should be noted that Paths 1, 2 and 3 had concrete edging and/or vegetation that restricted visitors from directly standing up against the fence lines (Figures 2 and 3). Ambient noise level

Table 2. Ethogram of visitor behaviours. Adapted from Chiew, Butler, et al. (2019) and Chiew et al. (2020).

Behaviour	Description
Loud vocalisations	Shouts, screams, squeal, cry or loud whistles.
Looming	Leaning on or over the enclosure barriers to view animals in the water or on land.
Sudden movement	Running, waving or jumping towards or at the penguin(s) and/or enclosure.
Throwing objects	Tossing any food, maps, sticks or other inanimate objects at penguin(s) or into the enclosure.
Standing on ledge	Upright position, stationary, and on a ledge or enclosure structure (i.e. sign/concrete ledge) to view penguins
Passively observing	Upright position, stationary, and viewing penguins and/or their enclosure. Not talking.
Walking	Moving at a regular pace by lifting and setting down each foot in turn, never having both feet off the ground at once.
Walking on ledge or signage	Moving at a regular pace by lifting and setting down each foot in turn while on the concrete ledge or signage of the enclosure.
Taking a picture	Using a phone or other camera device to photograph the penguins.
Crouch	Positioned lowered to the ground where the knees are bent, and the upper body is brought forward and down.
Entered visitor viewing hide	Visitor(s) went into the provided visitor viewing hide at the top of the enclosure to view penguins.
Other	Any other behaviour not described e.g. copying penguin vocalisations, sitting on enclosure signage or bench, hit enclosure signage, touching pool water, climbing enclosure structures.

was recorded continuously using a sound level data logger (Standard ST-173) which was placed inside the penguin enclosure on top of the boat shelter.

Statistical analysis

Visitor variables were only recorded on days the exhibit was open. The sum of adults and children were used to calculate visitor number totals. The sum of visitor behaviours displayed was used to calculate visitor behaviour frequencies for each day. Both visitor numbers and visitor behaviour frequencies were then averaged for each day and hour (per day), respectively, with between day standard deviation or dot histogram of daily values as a measure of variance. Ambient noise level was continuously recorded on all study days and so, was averaged over the 2-day treatment imposition periods to obtain a single summary value.

Each penguin behaviour measurement was averaged over the two days of each treatment imposition period, to obtain a single summary value for each 2-day imposition period. The percentage of penguins visible was calculated by totalling the number of penguins recorded visible each day divided by the total number of counts of penguins present each day (i.e. six \times number of samples taken on the day), then multiplying by 100, and finally averaging over the two days of each treatment imposition period. The percentage of penguins observed in each 'Zone' was handled in a similar manner whereby the total number of penguins recorded visible in each zone each day was divided by the total number of counts of penguins present each day, before being multiplied by 100. For animal behavioural states, the percentage of visible penguins observed displaying each behavioural state was calculated by totalling the number of penguins recorded in each behavioural state each day divided by the total number of penguins recorded visible each day, and then multiplying by 100. Animal behavioural events were handled in a similar manner whereby the total number of penguins displaying each behavioural event each day was divided by the total number of penguins visible within each 30 s period per day. These animal behaviour measures were subsequently averaged over the 2-day imposition periods of each treatment to obtain a single summary value. For FGM, the daily average for each known individual or pairs was calculated, and then all samples were averaged over the two days for each treatment imposition period to obtain a single summary value for the entire population.

Prior to statistical analysis, the summary values for animal behaviour (state and events), were angularly transformed. This ensured that the residual variation was similar in all treatments, and the distribution of residuals had minimal skewness. No transformation was required for ambient noise level. Furthermore, there were two '2-day treatment imposition periods' that had no penguins visible and as a result were removed before any analyses were performed on the animal behavioural state and event data. In other words, a total of only eight imposition periods out of the 10 were analysed, namely the periods when there were penguins visible.

The 2-day summary values were used as the unit of analysis in all statistical analysis. All animal measurements and ambient noise level were analysed as a five replicate (percentage of penguins visible and in specific areas; FGM; ambient noise), or as a four replicate (animal behavioural states and events), two-treatment analysis of variance (ANOVA) for a fully randomised design. The weather variables were 2-day averages

of daily observations from the Greta Point (Wellington) weather station, that is located three kilometres from the Wellington Zoo. A quadratic temporal effect was identified. So, weather variables and/or temporal variables were included as covariates whenever the covariates provided an appreciable improvement to the precision of the statistical analysis. With some penguin measurements, that had more discrete distributions because of low occurrence, the usual test for treatment difference based on the *F* distribution of the *F* statistic was replaced by a non-parametric permutation test. The non-parametric permutation used the same *F* statistic, but the *P*-value was calculated using permutations of the data values rather than comparing the value with an *F* distribution (VSN International 2015). Statistical analysis was carried out using the ANOVA directive and APERMTEST procedure of the GenStat 19.1.2 statistical package.

Results

Visitors

When the penguin exhibit was open to visitors, an average of 200 visitors were observed at the exhibit per day (Table 3). Visitors primarily viewed penguins from the visitor viewing pier which had an average of about 76 visitors observed in this area per day and depending on the day, varied from about 10 to 130 visitors (Figure 4). The adjacent area to the viewing pier, Path 1, had an average of 71 visitors observed each day and varied from about 30 to 120 visitors, making it the next section most used by visitors to view penguins (Figure 4). Path 2 and 3 had an average of 13 and 40 visitors each day, respectively. Visitors also displayed a variety of behaviours when the penguin exhibit was open and the most frequently observed behaviours were walking, looming, loud vocalisations, and sudden movements (Table 3). No effect of treatment was found on ambient noise level where the average was about 54 dB for each treatment ($F = 0.83$, d.f. = 1,8, $P > 0.05$).

Table 3. The average number of visitors and frequency of visitor behaviours recorded (seven 30 min observation blocks each day) when the little penguin exhibit was open to visitors.

Visitor variables	Average	Standard deviation ^a
Visitor present at the exhibit (<i>per day</i>)		
Total	200	88
Adults	125	64
Children	75	44
Behaviour (<i>Frequency per hour</i>)		
Loud vocalisations	21	16
Looming	32	23
Sudden movement	15	14
Throwing object(s)	0.029	0.090
Standing on ledge	11	8.6
Passively observing	11	5.9
Walking	37	18
Walking on ledge/sign	2.4	2.5
Taking a picture	3.7	3.8
Crouch	1.3	1.4
Entered viewing hide	4.2	4.4
Other	9.8	11

^aCalculated using between day variation.

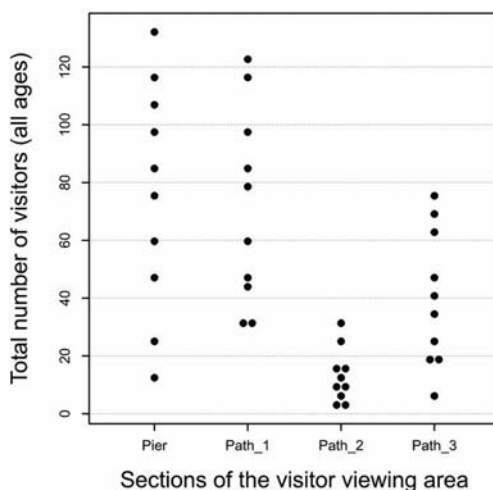


Figure 4. Dot histogram of the total number of visitors (all ages) present in each section of the visitor viewing area on days when the penguin exhibit was open. Each dot represents observations from a single day.

Little Penguin behaviour

Depending on the day, the average percentage of penguins visible in Zone 1 varied from 0% to about 54% and varied from 0% to about 35% in Zone 3 (Figure 5). The overall average percentage of penguins visible was 17% and 15% when the exhibit was open and closed, respectively (Table 4). When the penguin exhibit was closed to visitors, the percentage of penguins observed in Zone 1 increased from about 1% to 9% ($F = 13.83$, d.f. = 1,5, $P = 0.014$) and there was some indication of an increase in Zone 2 (1% to 3%; $F = 5.35$, d.f. = 1,5, $P = 0.069$; Table 4). There was no effect of closing the exhibit on other penguin behaviours ($P > 0.05$; Tables 4 and 5).

Little Penguin stress physiology

Closure of the exhibit had no effect on FGM concentrations ($F = 2.41$, d.f. = 1,6, $P > 0.05$, Table 5).

Discussion

This experiment examined the effects of visitor presence on zoo-housed little penguins. We found that the percentage of penguins close to the visitor viewing pier (Zone 1) was the only behaviour that was affected by the closure of the exhibit. No effect of visitor presence or absence was found on FGM concentrations. The limited change in behaviour may suggest that visitor presence had minimal or no substantial effect on penguin behaviour. However, the reduced percentage of penguins in Zone 1 when the exhibit was open to visitors indicates that there was increased avoidance of the visitor viewing pier by the little penguins. Since the visitor viewing pier was the main area where visitors viewed the penguins, this finding suggests that the penguins may be fearful of close visitor contact or

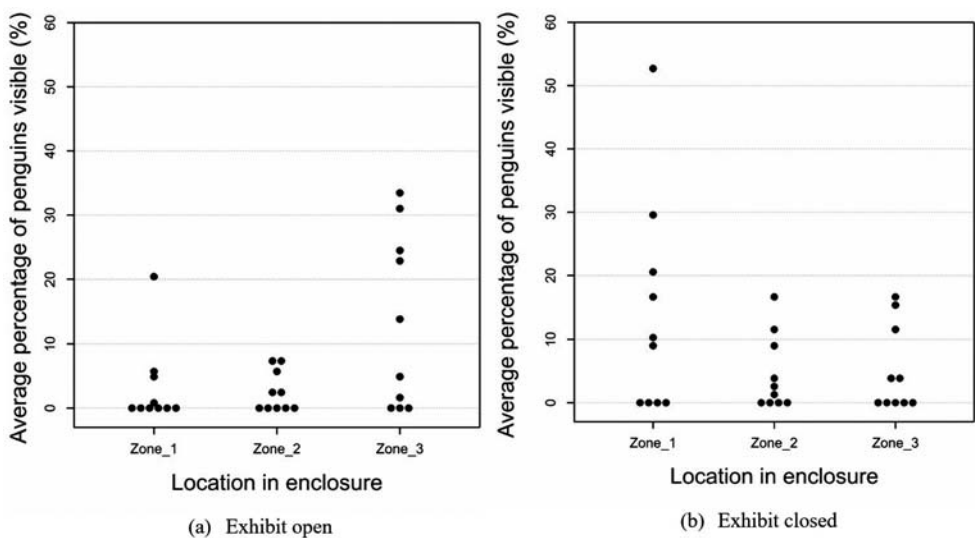


Figure 5. Dot histograms of the average percentage of penguins visible (%) in each location in the enclosure (Zone 1, 2 and 3) when the penguin exhibit was **(A)** open to visitors (visitor presence) and **(B)** closed to visitors (visitor absence). Each dot represents observations from a single day.

Table 4. Effects of the ‘visitor presence’ and ‘visitor absence’ on the average percentage of penguins visible and location in the enclosure (%).

Penguins visible	Covariates	Angular transformed			Back transformed (%)		P value
		Visitor presence	Visitor absence	s.e.d. ^f	Visitor presence	Visitor absence	
Zone 1	Quadratic temporal variate ^a + Rainfall ^b	6.3	18	3.0	1.2	9.1	0.014^d
Zone 2	Quadratic temporal variate ^a + Rainfall ^b	6.0	10	1.8	1.1	3.1	0.069 ^d
Zone 3		18	11	7.4	9.3	3.6	0.37 ^e
Overall	Quadratic temporal variate ^a	24	23	7.4	17	15	0.88 ^c

Note: No days were excluded for this analysis (i.e. all 10 imposition periods were included, 20 days).
^aIndicates quadratic response to a temporal variate response (1st pair of days (1st experimental unit) = 1, 2nd pair of days (2nd experiment unit) = 2, ... , 10th pair of days (10th experimental unit) = 10).
^bAverage rainfall for the 2-day treatment imposition periods obtained from Greta Point, Wellington meteorological station.
^cP value was calculated using a F test based on 1 and 6 degrees of freedom.
^dP values were calculated using F tests based on 1 and 5 degrees of freedom.
^eP value was calculate using a F test based on 1 and 8 degrees of freedom.
^fs.e.d. denotes standard error of difference.

close visitor viewing proximity. It is well established that avoidance behaviours are an indicator of fear of humans in animals (Hemsworth et al. 2018; Sherwen and Hemsworth 2019). Furthermore, previous research has found that little penguins (*Eudyptula novae-hollandiae*) in Australian zoos showed increased avoidance of the visitor viewing area when visitors were present, in close viewing proximity or when visual contact with visitors was unobstructed (Sherwen et al. 2015; Chiew, Butler, et al. 2019; Chiew et al. 2020). Zoo-housed African penguins (*Spheniscus demersus*) have also been shown to avoid and

decrease time spent in their pool when visitors were present in a pool adjacent to the penguin pool, especially in large numbers (Ozella et al. 2014). It has also been found that in the wild, little penguins avoid areas that visitors occupy such as visitor paths and areas of high human traffic (Weerheim et al. 2003; Giling et al. 2008; Shaughnessy and Briggs 2009). These studies support our interpretation that close visitor contact or viewing proximity may be fear-provoking for the little penguins in the present study.

This avoidance response by the little penguins when visitors were present may be because the visitor viewing pier extended out about 2 m over the pool and thus, positioned visitors on the pier above the level of the penguins in the enclosure. Also, one of the most observed visitor behaviours was looming, particularly at the viewing pier and at the fence line in 'Path 1' which was also in Zone 1. Therefore, visitors positioned above penguins in the enclosure when on the pier and the opportunities to lean on or over the enclosure barriers, may have been perceived as threatening and thus, potentially fear-provoking for the penguins when in Zone 1. As the smallest species of penguins, little penguins have numerous predators including aerial predators (Stahel and Gales 1987). Studies in the wild have also found humans standing over nesting penguins presented more of a threat, similar to an aerial predator, compared to people that kept low or crouched when observing penguins i.e. positioned at penguins' eye level or lower (Nimon 1997; Giese 1998; Holmes et al. 2005; Schuster 2010). It is worth noting that there were opportunities in Paths 2 and 3 for visitors to view penguins in close proximity. However, most visitors did not spend much time in these sections of the visitor viewing area, as indicated by the lower visitor numbers observed compared to the Pier and Path 1. This was likely because of vegetation and other structures (e.g. the boat) in the exhibit that obstructed the view between penguins and visitors on Paths 2 and 3.

Of the three experiments conducted by Chiew and colleagues (Chiew, Butler, et al. 2019; Chiew et al. 2020; present experiment), the most marked effects of visitors on penguin behaviours indicative of fear were observed in the experiment at Melbourne Zoo (Chiew, Butler, et al. 2019) and the present experiment at Wellington Zoo. In the former, closing the exhibit to visitors increased the percentage of visible penguins within 1 m of the main visitor viewing area by 28-fold (from 1% when the exhibit was open to 28% when closed). While in the latter (present experiment), closing the exhibit to visitors increased the percentage of penguins visible in Zone 1 (within 4 m of the main visitor viewing area) by 9-fold (from 1% when the exhibit was open to 9% when closed). In the experiment by Chiew et al. (2020) at Taronga Zoo, covering the main visitor viewing area window resulted in a slight increase in the percentage of penguins in the area near this main window, by about 25% (from 12% when the window was uncovered to 15% when covered). In the experiment at Melbourne Zoo, it was also found that restricting visitors from closely approaching the pool increased the percentage of visible penguins within 1 m of the main visitor viewing area by about 1300% (from 1% with unrestricted approach to the pool to 14% when close approach was restricted) (Chiew, Butler, et al. 2019).

Both enclosures at Melbourne and Wellington Zoo when uncontrolled, allowed visitors in the main viewing areas opportunities, if they chose, to closely approach and loom over the pool edge. In contrast at Taronga Zoo, the visitor viewing area was primarily below the level of penguins in the pool and penguins were viewed underwater through tall glass windows. These considerations, together with the differences between zoos in

Table 5. Effects of ‘visitor presence’ and ‘visitor absence’ on the average percentage of visible penguins (%) displaying each behaviour (states and events) and stress physiology.

Penguin behaviour	Covariates	Angular transformed			Back transformed (%)		<i>P</i> value ^b
		Visitor presence	Visitor absence	s.e.d. ^d	Visitor presence	Visitor absence	
<i>States</i>							
Huddling (on land)	Rainfall	24	27	9.6	16	20	0.78
Surface swimming		8.0	25	7.7	1.9	18	0.074
Diving		0.76	1.5	0.78	0.018	0.066	0.54 ^c
Resting (on land)	Maximum temperature	0.78	2.7	1.2	0.019	0.22	0.18
Idle (on land)		58	50	8.0	71	58	0.36
Locomotion (on land)		16	16	3.0	7.7	7.1	0.86
Vigilant (on land)	Maximum temperature	23	19	7.0	15	11	0.60
<i>Events</i>							
Preening (on land)	Rainfall	27	34	4.6	20	31	0.18
Preening (in water)		4.7	8.1	3.5	0.67	2.0	0.38
Allopreen		2.4	2.0	1.3	0.17	0.12	0.77
Agonistic		5.4	5.3	1.8	0.89	0.85	0.95
Bathing		5.6	12.2	5.0	0.95	4.5	0.24
Body Shake (on land)		9.2	8.2	0.73	2.6	2.0	0.26 ^c
Head flick/shake (on land)		15	15	1.5	6.6	6.6	0.97
Beak movement display (on land)		2.8	2.4	2.1	0.24	0.18	0.86
Social interaction		4.2	2.8	1.7	0.53	0.24	0.44
Scratch (on land)	2.2	11	4.2	0.15	3.4	0.090	
Scratch (in water)	3.3	7.0	3.2	0.33	1.5	0.290	
Other	5.8	4.3	1.1	1.0	0.55	0.23	
<i>Stress physiology</i>							
FGM concentration (ng/g)	Quadratic temporal variate ^a + Gust speed	3246	3635	259	–	–	0.19

Note: Two imposition periods were excluded for these analyses, except for FGM concentrations (i.e. only imposition periods where the percentage of penguins visible was greater than 0% were included). Windspeed (km/h) is the daily vectorial movement of the atmosphere at or near the surface of the land (or sea), averaged over each 2-day period. Gust speed (km/h) is the daily maximum/strongest wind vector, averaged over each 2-day period.

^aIndicates quadratic response to a temporal variate response (1st pair of days (1st experimental unit) = 1, 2nd pair of days (2nd experiment unit) = 2, ... , 10th pair of days (10th experimental unit) = 10).

^bP values are calculated using F tests based on 1 and 5 degrees of freedom for all measurements with a covariate(s), and 1 and 6 degrees of freedom without a covariate.

^cP values calculated using permutation test.

^ds.e.d. denotes standard error of difference.

avoidance behaviour from the main visitor viewing area described in the previous paragraph, suggest that the viewing height of visitors relative to the position of the penguins may influence the magnitude of the fear response of penguins. Indeed, as Chiew, Butler, et al. (2019) have suggested, close approach and looming by visitors are likely to be perceived by little penguins as an aerial predatory threat. However, it should be recognised that there are other differences between these three experiments that may have also influenced the apparent difference in fear responses in little penguins to the uncontrolled presence of visitors at Melbourne Zoo, Wellington Zoo and Taronga Zoo. These differences include aspects of enclosure design, previous experience (e.g. captive bred or wild bred) and genetics as well as the behavioural measurements and behaviour sampling methods, in addition to the differing nature and intensity of visitor interactions in these experiments (Mathews et al. 2005; Peucker et al. 2009; Conway 2011; Mason

et al. 2013; Grosser et al. 2015; Grosser et al. 2016; Grosser et al. 2017; Sherwen and Hemsworth 2019).

Like animals in other captive settings, research has shown that enclosures that provide zoos animals with a level of choice and control over the interactions with visitors, for example by providing an area to retreat, can help minimise visitor-induced stress (Owen et al. 2004; Ross 2006; Morgan and Tromborg 2007). Wellington Zoo's penguin enclosure was heavily vegetated with Zone 3, hosting physical structures such as most of the vegetation in the enclosure, a partially upturned boat and nest boxes. It is likely that this zone with its structures and distance from the visitor viewing pier, provided both physical and visual separation from most of the visitors. Consequently, the design of Wellington Zoo's penguin enclosure may have helped minimise the intensity of close visitor contact. It also suggests that having viewing features in the exhibit that allow visitors to view penguins in close proximity, may be futile since penguins would move away and thus, likely reduce visitor viewing experience. As previously mentioned, research in Australian zoos has shown that increased separation between visitors and little penguins reduces penguin fear responses towards visitors and has no detrimental effect on visitor experience (Chiew, Butler, et al. 2019; Chiew, Hemsworth, et al. 2019).

FGM concentrations were not affected by treatment which suggests that visitor presence had minimal effect on the overall welfare of the little penguins. One explanation is that a more sustained period of treatment, greater than two days, is required to detect a measurable change in FGM arising from closing the exhibit, similar to that found and suggested by Chiew, Butler, et al. (2019). It is well established that adrenal activity increases fairly quickly in response to stressors. In little penguins, FGM concentrations increase approximately 7 h after experiencing a stressor (Sherwen and Fanson 2015). However, there is less information about how long it takes for adrenal activity to decrease after a long-term stressor is removed like visitors. Secondly, the opportunity for choice and control over their interactions with visitors, as a result of the design of the enclosure, may have ameliorated the need for the activation of the hypothalamo–pituitary–adrenal axis in little penguins arising from uncontrolled visitor contact.

Several weather variables were found to be useful covariates for improving the precision of the statistical analyses for examining the effects of visitors. This is an indicator that the behaviour and physiology of little penguins were strongly affected by weather. This is not surprising considering the experiment was conducted between the end of Autumn (May) and the start of Winter (June), with the change in seasons generally associated with shifts to lower temperatures and higher rainfall. However, weather reports also showed that Wellington experienced very unsettled weather patterns during the Autumn and Winter of 2018 (Pezza et al. 2018a, 2018b). Research on various wild penguin species have shown that colder temperatures can increase sleeping and huddling behaviour; severe rainfall can reduce breeding success and survivability; and increased wind speeds, particularly during storms that cause rough seas with high waves, can decrease activity, foraging success and time spent diving and foraging (Culik et al. 1989; Dewasmes et al. 2001; Gilbert et al. 2008; Demongin et al. 2010; Ganendran 2011; Dehnhard et al. 2013; Berlincourt and Arnould 2015; Ganendran et al. 2016; Saraux et al. 2016). Additionally, harsh inclement weather such as blizzards, extreme high and low temperatures, storms and heavy rain, have been associated with increased corticosterone concentrations in various bird species including penguins (Wingfield et al.

1983; de Bruijn and Romero 2013; Thierry et al. 2013; Ozella et al. 2017; de Bruijn and Romero 2018; Scheun et al. 2020). Consequently, further research on the effects of weather on zoo-housed little penguin behaviour and physiology is required.

In our research across two Australian zoos and now a zoo in New Zealand, we have found there are some common characteristics of visitor contact that zoo-housed little penguins may find fear-provoking. These characteristics include close visitor contact or the close viewing proximity of visitors (Sherwen et al. 2015; Chiew, Butler, et al. 2019; Chiew et al. 2020). While having close contact with penguins including close human contact from above may be beneficial for the viewing experience of visitors, these characteristics of visitor contact may increase the likelihood of potentially threatening visitor behaviours occurring (e.g. banging on enclosure features, looming behaviour and sudden movement). As a result, visitors are more likely to be perceived as threatening and thus, increase little penguins' fear responses (Sherwen et al. 2015; Chiew, Butler, et al. 2019; Chiew et al. 2020). These characteristics of human contact are also consistent with studies on other species of zoo-housed penguins and wild penguins (Klomp et al. 1991; Wienecke et al. 1995; Nimon 1997; Giese 1998; Weerheim et al. 2003; Holmes et al. 2005; Giling et al. 2008; Shaughnessy and Briggs 2009; Schuster 2010; Ozella et al. 2014).

Close visitor contact may be mitigated by positioning visitors further away from the enclosure boundary or by reducing the perceived close proximity of visitors in little penguins (Chiew, Butler, et al. 2019; Chiew et al. 2020). This highlights some important practical measures that should be considered to manage visitor-penguin interactions in both zoo and wild settings. For example, increased separation between visitors and little penguins, whether that be by using a physical barrier to push visitors back from the enclosure or designing enclosures in a way that allows for this (Chiew, Butler, et al. 2019). Zoos can also consider reducing the perception of the close viewing proximity of visitors by positioning visitors below penguins, by providing areas for penguins that are visually hidden from visitors or by using one-way viewing windows (Chiew et al. 2020). These practical measures can ultimately result in the improvement in the welfare of penguins as well as have no detrimental effect on visitor viewing experience (Chiew, Butler, et al. 2019; Chiew, Hemsworth, et al. 2019; Chiew et al. 2020). However, the effectiveness of one-way viewing windows to regulate visitor-penguin interactions to improve the welfare of penguins without negatively affecting visitor experiences has not yet been experimentally examined, and thus requires further investigation. This can be examined in aquarium settings which, like many zoos, commonly house various penguin species and utilised glass viewing windows.

Conclusions

Little penguins (*Eudyptula minor*, *Kororā*) at Wellington Zoo showed an avoidance of the visitor viewing pier when the exhibit was open to visitors which suggests that these penguins may be fearful of close visitor viewing proximity. These results suggest viewing features that are designed to allow close viewing proximity, such as piers overhanging the exhibit, may be ineffective in improving visitor experience since little penguins are likely to avoid these features when visitors are present. This avoidance of visitors may be exacerbated by visitors being perceived as a predator while on viewing features that position visitors close to and above the penguins. Consequently, zoos exhibiting little penguins should design the enclosure and visitor viewing areas so that visitors are set

back from the enclosure boundary or by obscuring the penguins' view of visitors to minimise the potential fear responses of the penguins to zoos visitors.

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